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Structure and functional characteristics of the meiofauna community in highly
unstable intertidal mudbanks in Suriname and French Guiana (north Atlantic
coast of South America)

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Abstract

The north Atlantic coast of South America is influenced by the Amazon River. This coast is considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River. The mobility of the sediment imposes a geomorphological dynamic with a rapid change of shoreline and fast alternation of facies types of the sediment. This study first describes the spatial and functional structure of meiofauna communities of highly unstable intertidal flats along coasts of French Guiana and Suriname in relation to environmental variables. Six sampling sites, composed mainly of muddy sediment, were located 700 km (Kourou) to 1200 km (Nickerie) from the mouth of the Amazon River. The granulometry, chlorophyll *a* biomass, prokaryote abundance, percentage of organic matter, meiofauna abundance and feeding guilds of nematodes in sediment stations were independent of the distance of the Amazon River mouth and likely were more influenced by the local dynamism of migration of mudbanks. Meiofauna was not more abundant when the sediment was dominated by the finest sediment particles and also when chlorophyll *a* and prokaryotes, potential prey of meiofauna, were greater. However, as a percentage, small nematodes (biomass of $0.07 \pm 0.001 \mu\text{g ind}^{-1}$), which are mainly epigrowth-feeders, were more abundant in very fluid mud. Local granulometry and organic matter content appeared to be driving factors of the size structure and functional characteristics of nematodes. Despite the high instability of mudflats, chlorophyll *a* biomass and meiofauna abundance always tended to be higher toward other world areas. No foraminifera among the six stations of the study were found. Very fluid mud with physical instability of sediment caused a large perturbation to the settlement of meiofauna; the least amounts of chlorophyll *a* biomass and prokaryotic and meiofauna abundances were found there. Thus, the probable mobility of sediment may select for smaller meiobenthic organisms, mainly epigrowth-feeders nematodes, and disturb the

larger organisms in the sediment, and, therefore, they would not permit the settlement of the foraminifera. In addition, no non-permanent meiofauna largely was found in the sediment.

1. Introduction

The coast between the Amazon and Orinoco Rivers (1500 km) in South America is considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River ($754 \text{ Mty}^{-1} \pm 9\%$) (Martinez et al., 2009). Thus, a large amount of fluid mud is transported from the Amazon River mouth in a north-western direction along the coasts of the Guianas, including French Guiana and Suriname, by a complex interaction of waves, tidal forces, and coastal currents. These complex interactions result in the formation of a series of large mudbanks that are distributed in at least 15 units 10–60 km long and 20–30 km wide and migrate 1 km y^{-1} (Allison et al., 2000). They impose a geomorphological dynamic leading to rapid changes of shoreline and fast alternation of facies type (Anthony et al., 2010). The intertidal area, bordered by mangroves, represents approximately 5% of the entire mudbank. Although these emerged mudflats are unique in the world considering their high dynamic processes and particular instability, the diversity and structure of communities as well as food web functionality associated with these mudbanks are mostly unknown.

Intertidal soft sediment habitats rank among the most productive ecosystems on Earth, largely owing to the primary production of highly diverse assemblages of benthic diatoms (Underwood and Kromkamp, 1999). Indeed, at every low tide, the intertidal flats are rapidly covered by mats of microalgae (microphytobenthos [MPB]) (Underwood and Kromkamp, 1999). Diatoms have the ability to migrate through fine sediments according to the tidal and daily irradiation cycles in order to find optimal light conditions for their growth. The MPB constitutes a complex biofilm in association with prokaryotic communities, mainly composed of bacteria in the sediment surface (van Duyl et al., 1999). These prokaryotes play a fundamental role through the degradation and remineralisation of nutrients. The components of biofilm (MPB and prokaryotes) are considered key ecosystem engineers in food webs. In

addition, diatoms are known to be important trophic sources for many benthic organisms (meiofauna and macrofauna), and the prokaryotes can represent a complementary food source for meio- and macrofauna (Moens and Vincx, 1997; Pascal et al., 2008a, b; Pascal et al., 2009).

Meiobenthos occurs in all types of sediments and is thus able to reside in a wide variety of habitats (subtidal and intertidal areas). Nevertheless, the texture of the sediment is an important variable for structure and composition of meiobenthic assemblages (Schwinghamer, 1981; Semprucci et al., 2010; 2011). Abundance of benthic organisms is generally higher toward fine grains due to a concomitant increase of food availability (Balsamo et al., 2010; Heip et al., 1992). Meiofauna is generally considered to constitute recurrent taxa, such as nematodes, copepods, and foraminifera, and non-permanent taxa, such as small gastropods, small bivalves, and small annelids. In mudflats, nematodes are consistently considered the most abundant meiobenthic taxa (Boucher and Lamshead, 1995). Some authors have suggested that the ecological significance of nematodes is crucial in terms of foodweb relationships (reviewed in Balsamo et al., 2012; Heip et al., 1985; Platt and Warwick, 1980), production of detrital organic matter, and recycling of nutrients, thereby enriching the coastal waters to support marine benthic production. Nematodes are functionally diverse, as they can be herbivores, bacterivores, deposit feeders, epigrowth feeders, or predators (Pascal et al., 2008b; Rzeznik-Orignac et al., 2003).

The spatial structure of meiofauna assemblages has been well studied in temperate mudflats (Pascal et al., 2008b; Rzeznik-Orignac et al., 2003) and tropical mangrove areas (Alongi, 1987; Chinnadurai and Fernando, 2007; Debenay et al., 2002; Xuan et al., 2007). Nevertheless, studies of bare tropical mudflat meiofauna are scarce and completely absent for the Guiana coast areas submitted to high dynamic processes, leading to a strong instability rarely met among coastal ecosystems.

The present study first describes the spatial and trophic functional structure of meiofauna communities of intertidal flats along the French Guiana and Suriname coasts in relation to environmental variables such as granulometry, chlorophyll *a* biomass, prokaryote abundance, and percentage of organic matter in sediment. The sampling stations are influenced by the Amazon flume, considered the largest and muddiest river in the world, and the choice of the stations presented a gradient of influence of the river from east to west (from French Guiana to Suriname). Second, three types of mud facies (fluid mud, moderately compacted mud, and compacted mud) were sampled on the intertidal mudflats of Awala (French Guiana), and their meiofauna communities were compared. We hypothesised that in highly unstable intertidal mudbanks:

- 1) Compositions and abundances of meiofauna were different according to the grain size and particularly the fraction of fine sediment particles
- 2) Meiofauna was more abundant when MPB biofilm containing diatoms and prokaryotes, which are potential prey for meiofauna, was more abundant.

2. Materials and methods

2.1. Study sites

The intertidal mudflats studied are located along the French Guianese coast in front of the city of Kourou and village of Awala-Yalimapo and on the Surinamese coast near the village of Warappa and city of Nickerie (Fig. 1). All stations were sampled in April 2012 (wet season) at low tide in the upper area of the intertidal mudflats. The tides of the considered coast sections are semidiurnal with a tidal range of 0.8 m (neap tides) to 2.9 m (spring tides).

The median sediment grain size was characterised using a Malvern Mastersizer 2000 (Malvern Instruments, Ltd., UK) (size range 0.02–2000 μm). This analysis allowed definition of different sediment textural groups by the relative abundance (percent volume) of mud

(diameter < 63 µm) and sand (diameter between 63–2000 µm) according to the Udden-Wentworth scale. Data processing was performed using the GRADISTAT program (Blot and Pye, 2001).

The sampled mudflat at Kourou (05°10'40.45"N; 52°38'53.74"W) is the closest study site to the Amazon River mouth at a distance of 700 km (Fig. 1). At Kourou, one station was sampled (Table 1). The Awala mudflat station is located 850 km from the Amazon River mouth (Fig. 1). On this mudflat, contrary to other sites, samples were collected at three stations along a transect parallel to the coastline, presenting an alternation of facies type: Station A (St A) (05°44'44.6"N; 53°55'36.2"W), with very fluid mud (very soft mud); Station B (St B) (05°44'44.7"N; 53°55'07.2"W), with moderately compacted mud (soft mud) and Station C (St C) (05°44'44.6"N; 53°54'57.8"W), with compacted mud just before young mangroves. Warappa and Nickerie are located 1000 km and 1200 km from the Amazon River mouth, respectively (Fig. 1). One station per site was sampled at Warappa (soft mud) (05°59'32.9"N; 54°55'50.1"W) and at Nickerie (soft mud) (05°59'09.9"N; 56°53'03"W).

For each triplicate sample, the top 2-cm layers from three 15-cm diameter cores were sliced and gathered together. Each sediment sample was homogenised directly in the field in a sterile box and was subdivided for further analysis (storage conditions differed according to parameters).

2.2. Environmental parameters

Organic matter content (OM) (weight loss after incineration) of the sediment was estimated by weight loss at 450°C for 24 h (Wollast, 1989) from three replicated cores (deep frozen for later analysis). The OM was expressed as the percentage of total matter.

Three replicated cores were used for algal biomass determination, which was assessed using chlorophyll *a* (Chl *a*) as a proxy and measured using fluorometry (640 nm, Turner TD 700, Turner Designs, USA) according to the method of Lorenzen (1966). Extraction of Chl

awas obtained using freeze-dried sediment extracted at night in darkness in 4°C, 90% acetone and centrifuged (10 min, 3500 g, 8°C). The Chl a biomass was expressed as $\mu\text{g}\mu\text{g}^{-1}$ dry weight (DW) sediment or $\mu\text{g Chl a m}^{-2}$.

Heterotrophic prokaryotic abundance (PA) was quantified by flow cytometry according to Lavergne et al. (2014). Sub-samples of the top 2 cm of the sediment were fixed with 0.2- μm filtered formaldehyde (vol/vol) (2% final concentration) and stored at 4°C up to 3 months before analysis. Thawed samples were homogenised, prepared, and analysed as follows: 1) Sample preparation and extraction: dilution (1:1000–1:2000) in a detergent mix (sodium pyrophosphate [0.01 M] + Tween 80 [0.1%]), vortexing step, and 30 min of incubation at 4°C. After the vortexing step, a sonication separation for 30 s (60W) in ice with a sonication probe (3 mm) was applied. An aliquot of the sample was stained with SYBRGreen I (1:10000) for 15 min in the dark and analysed by flow cytometry (see analysis details below); and 2) the remaining part of the sample was centrifuged at low speed (1 min at 1000 g at 4°C). The pellet was then resuspended in the detergent mix, and step 1 was repeated once. Each sample was analysed for 30 s at low flow speed with a FACS Canto II cytometer (3-laser, 8-color [4-2-2], BD Biosciences) using DIVA software. Fluorescent beads (Fluoresbrite Multifluorescent 1- μm microspheres, Polysciences, Germany) were added to each sample and simultaneously analysed. Stained cells were differentiated according to their green fluorescence (FL1) from SYBRGreen I staining and side-scatter properties (SSC). Picophytobenthic cells also were discriminated from heterotrophic prokaryotes by their red autofluorescence (FL3) and SSC properties and were excluded from final prokaryotic counts, measured on a gate SSC-FL1 (Marie et al., 2001). Accurate cell concentrations were performed using TruCount beads (BD-Biosciences) (excitation: red laser at 633 nm; emission: FL5 660/20 nm). Abundances were expressed as cells per cubic centimetre or millilitre of fresh sediment (cell cm^{-3} or cell mL^{-1} , respectively).

2.3. *Meiofauna abundance*

Meiofauna abundance and group composition were obtained from three replicated cores. The top 2 cm of sediment from each core were preserved in absolute ethanol (vol/vol). Samples (50 mL) were sieved through 50 μm before staining with rose Bengal and observation under a binocular loupe (Zeiss). A sample splitter (Motoda box as Rzeznik-Orignac et al., 2003) was used to obtain an aliquot containing at least 100 individual nematodes for the abundance estimation.

The abundance of other meiobenthic taxa (i.e., copepods and ostracodes) was too low to be evaluated in split samples and, therefore, was quantified using whole samples. Abundances were expressed as individuals per cubic centimetre (ind cm^{-3}) or individuals per 10 cm^2 (ind 10 cm^{-2}). The sizes (length and width) of nematodes were measured for at least 100 specimens picked haphazardly through a calibrated ocular micrometer. Three different size classes were made: small nematodes (mean length: $300 \pm 30 \mu\text{m}$; mean width: $18 \pm 5 \mu\text{m}$), medium nematodes (mean length: $695 \pm 130 \mu\text{m}$; mean width: $26 \pm 9 \mu\text{m}$), and large nematodes (mean length: $1500 \pm 160 \mu\text{m}$; mean width: $75 \pm 10 \mu\text{m}$). The biovolume was calculated using Warwick and Price (1979) formula: $V = 530LW^2$, where V = biovolume (nl), L = length (mm) and W = width (mm). Biovolume was then converted in biomass, considering specific density as $1.13 \mu\text{g nl}^{-1}$ (Wieser, 1960). The corresponding biomasses were: small nematodes: $0.07 \pm 0.001 \mu\text{g ind}^{-1}$, medium nematodes: $0.32 \pm 0.01 \mu\text{g ind}^{-1}$, and large nematodes: $5.73 \pm 0.01 \mu\text{g ind}^{-1}$.

From each of the three replicates, 100 nematodes were randomly withdrawn and mounted on slides in anhydrous glycerol to prevent dehydration (Seinhorst, 1959) and observed under a 100x oil immersion objective (Axioskop 2, Zeiss). All nematodes were then classified into four trophic groups according to Wieser (1953; 1960) as follows: 1A (selective

deposit-feeders), 1B (non-selective deposit-feeders), 2A (epigrowth-feeders), and 2B (omnivorous-carnivores).

2.4. Statistical analysis

In the results section, all values are presented as means \pm SD. Variations in environmental variables or meiofauna abundances according to the sites were tested using Fisher tests or Wilks-Lambda tests after testing for data normality. For non-normal data, Wilcoxon tests were applied. The relationships between environmental parameters and meiofauna were assessed by principal component analysis (PCA). Pearson's correlations were used to measure and test the correlations between environmental variables and meiofauna. These analyses were performed with the XLSTAT 2014 software.

3. Results

3.1. Environmental variables

At Kourou, sediment was classified as fine sandy medium silt (Table 1). The Awala mudflat stations presented an alternation of three facies types: St A with very fluid mud (very soft mud) and composed of fine sandy silt; St B with moderately compacted mud (soft mud) and composed of fine silt; St C with compacted mud and composed of fine silt (Table 1). Warappa mudflat sediment was composed of fine silt, while Nickerie mudflats were made up of very coarse sandy fine silt (Table 1). In summary, the median grain size (MGS) among the six sampling stations ranged from 5.4 to 11.0 μ m, and the percentage of mud in these six stations (81.0% at Kourou, 88.76% at Awala St A, 89.65% at Nickerie, and more than 99% at Awala St B, St C and Warappa [Table 1]) was independent of the distance to the Amazon River from east to west (from French Guiana to Suriname).

The percentage of OM mass in the sediment ranged from 4.4% (Kourou) to 6.2% (Warappa) (Table 1). Only one value for Kourou was significantly different from other stations (Wilcoxon, $p < 0.05$).

The mean Chl a biomass of the top 2 cm of the sediment varied from 7–19 $\mu\text{g Chl a g}^{-1}$ DW sediment (corresponding to 70–190 mg Chl a m^{-2}) (Fig. 2). The Chl a biomasses were the lowest at Kourou and Awala St A (large SD, no significant difference found between values, Fisher, $p > 0.05$), and the maximum Chl a biomass was recorded at Awala St B (significant difference between Kourou and Awala St B, Fisher, $p < 0.05$). Along the Awala transect, where facies was modified between St A to St C, the Chl a biomass was greatest in the intermediate moderately compacted muddy station (St B: $18.77 \pm 1.57 \mu\text{g Chl a g}^{-1}$ DW sediment) (significant difference between the three stations at Awala, Fisher, $p < 0.05$).

Heterotrophic prokaryotic (PA) cell abundance ranged from $1.8\text{--}4.4 \times 10^9$ cells mL^{-1} wet sediment in the 2-cm layer (Fig. 3). Prokaryotic cell numbers were lowest at the Kourou and Awala stations but higher at Nickerie (significant difference, Fisher, $p < 0.05$), despite a large abundance variability ($4.4 \times 10^9 \pm 1.36 \times 10^9$ cells mL^{-1}). Along the Awala transect, prokaryotes were less abundant at St A. At St B and St C, no significant differences were observed (Fisher, $p < 0.05$).

3.2. Meiofauna abundance

For the entire study area, total abundances of meiobenthos ranged from about 88–220 ind cm^{-3} (corresponding to 1760 ind 10 cm^{-2} to 4400 ind 10 cm^{-2} at Awala St A and Awala St C, respectively) (Fig. 4). The mean value for the six stations was 136 ind cm^{-3} .

Along the Awala transect, a gradient of total abundances of meiobenthos appeared. The lowest abundances were recorded in the very fluid mud station (St A), a medium value was recorded in the moderately compacted mud station (St B), and the highest abundances were

observed in the compacted mudstation located at the edges of mangroves (St C)(significant differences between St A, B, and C at Awala, Fisher, $p < 0.05$).

For all sampled stations, nematodes represented the most dominant taxon, contributing 73–92% of total meiobenthos abundance at Awala St A and Warappa, respectively (Figs.4 and 5). Copepods contributed 0.5–26% of the meiobenthos abundance in Warappa and Awala St A, respectively (Figs. 4 and 5). The other groups (ostracodes, plathelminthes, small bivalves, and small gastropods) accounted for a very low percentage of the meiobenthos (less than 1%). One exception included ostracodes representing 8% of the total abundance at the Warappa station, and, in parallel, at this same station copepods were at very low abundance (0.5%). Surprisingly, no foraminifera were found among the six study sites.

Along the Awala transect, the percentage of nematodes increased, while the percentage of copepods decreased from St A to St C (from 26% in very fluid mud to 8.7% in compacted mud before mangroves).

At all stations except Awala St A, the size class of medium nematodes (biomass of $0.32 \pm 0.01 \mu\text{g ind}^{-1}$) was the most dominant, contributing to 51–77% of total nematode abundance at Awala St B and Awala St C, respectively (Fig.6), with significant differences between Kourou and Awala St A, Nickerie and Awala St A, and Warappa and Awala St C ($p < 0.05$). Significant differences were observed for large nematode abundances between Nickerie and Warappa ($p < 0.05$). No significant difference was observed for small nematode abundances among all stations.

Along the Awala transect, the percentage of medium nematodes increased, while the percentage of small nematodes decreased from St A to St C from 44% in very fluid mud to 17% in compacted mud before mangroves (significant difference between three stations at Awala, Fisher, $p < 0.05$).

The proportion of nematodes gathered per trophic guilds was presented in Figure 7. Epigrowth-feeders (2A) were dominant in the different stations increasing in proportion through the granulometric gradient, with the lower proportion at Kourou (38 % of nematode community) and the maximum recorded at Awala St C (92 %) (significant difference, Fisher, $p < 0.05$). The second dominant feeding type was non-selective deposit feeders (1B), inversely proportional to 2A and ranging from 5 to 33 % at Awala St C to Kourou (significant difference, Fisher, $p < 0.05$). Selective deposit-feeders (1A) and omnivorous-carnivores (2B) represented an average proportion of 6 and 5 %, respectively. The medium and small nematodes belonged largely to epigrowth-feeders (2A) guild while large ones were from the 4 guilds, but the omnivorous-carnivores (2B) were represented by the large nematodes.

3.3. Relationship between environmental parameters and meiofauna

Factor plans 1, 2, 3, and 4 of the PCA together explained 97.0% of the observed variability in each sample (Fig. 8) (axis 1: 59.8%, axis 2: 18.1%, axis 3: 11.0%, and axis 4: 8.1%). The variables OM content, small and large nematode abundances, and percentage of mud and sand, and the 4 feeding guilds of nematodes were represented by factor plan 1. The variables Chl a biomass, copepod, and ostracodes abundance were represented by factor plan 2. The PA abundance was represented by factor plan 3, and medium nematode abundance was represented by factor plan 4.

Only significant correlations were presented here and in Table 2: the OM content was positively correlated with small nematode abundance, 2A feeding type and percentage of mud, and negatively correlated with 1A feeding type, 2B feeding type and percentage of sand (Table 2; Fig. 8). The % of mud was correlated with 2A feeding type but negatively correlated with 1A, 1B and 2B feeding type and % of sand. The result of % of sand was inverted as above. Small nematode abundance was positively correlated with 2A feeding type and percentage of mud but negatively correlated with 1A feeding type, 2B feeding type and % of

sand. Large nematodes abundance was positively correlated with 2B and 1A feeding type and percentage of sand, but negatively correlated with 2A feeding type and % of mud. Moreover, copepod abundance was negatively correlated with ostracodes abundance (Table 2; Fig. 8). 1A feeding type was positively correlated with 2B feeding type but negatively correlated with 2A feeding type. 1B feeding type was negatively correlated with 2A feeding type and finally, 2A feeding type was negatively correlated with 2B feeding type.

The PCA exposed a clear separation of different clusters corresponding to the sampling sites, driven by their abiotic and biotic parameters of the four factor plans (Fig. 8, factor plan 4 not shown). Kourou site exhibited the lowest percentage of mud (81% mud), lowest OM content, lowest Chl a biomass and the lowest nematode abundance of small one. The same station exhibited the highest percentage of sand (19 %), a part of large nematode abundance and 1A, 1B, 2B feeding type. In contrast, the Awala St B and St C were very muddy (100% mud) and showed high OM content, Chl a biomass and the highest percentage of 2A feeding type and, at St B, high abundance of small nematodes and presence of copepods. The Warappa station was mainly represented in factor plan 2 and was characterised by the highest abundance of ostracodes and average Chl a biomass; it was slightly represented in factor plan 1, characterised by a very muddy sediment and rich OM. Nickerie was represented in factor plans 2 and 3, characterised by high Chl a biomass and prokaryotic and copepod abundances. Awala St A was well represented in factor plan 3, characterised by the lowest PA abundance. In addition, Awala St A exhibited 89% mud, the lowest Chl a biomass, the lowest prokaryotic and meiofauna abundances, but the highest proportion of small nematodes and copepods.

4. Discussion

The coasts of French Guiana and Suriname in South America are considered the muddiest in the world due to the enormous suspended sediment input from the Amazon River.

Our six sampling sites were located 700 km (Kourou) to 1200 km (Nickerie) from the mouth of the Amazon River.

Our work clearly demonstrated that the distribution of the environmental parameters measured (median grain size, OM content, Chl a biomass, and prokaryotic cell abundance) was independent of the distance of the Amazon River mouth among sampling sites of the four study sites. The grain size ranged from 5.4–11 μm among the six sampling sites, and the percentage of the mud in these six stations was independent of the distance to the Amazon River, from east to west (from French Guiana to Suriname). The environmental parameters probably were more influenced by the local dynamism of the migration of the mudbanks (Allison et al., 2000). Indeed, mudbanks are under strong influence of waves, tides, wind, and coastal currents, generating the movement of fluid mud, which moves more than 1 km y^{-1} (Allison et al., 2000). These migrant banks impose a geomorphological dynamic, leading to rapid, local changes of the shoreline (Anthony et al., 2010). In the same manner, distribution and structure of Chl a and meiofauna were independent of the distance to the Amazon River. Further studies are needed at a smaller scale to measure the physical conditions of the resuspension of the sediment (i.e., bed friction velocity) (Dupuy et al., 2014; Orvain et al., 2014).

The postulated hypothesis tested was that compositions and abundances of meiofauna were different according to the grain size and particularly the fraction of fine sediment particles. In the literature, muddy sediments are characterized by high meiofaunal, and in particular, nematode abundances (Giere, 2009; Heip et al., 1985). Yamanaka et al. (2013) found an increase of meiofauna abundance with increasing particle size (183–230 μm median particle size) on shallow- and intermediate-slope beaches. Coull (1999) argued that abundance values tend to be highest in organically enriched muds but lowest in clean sands. This postulated hypothesis is not corroborated with the present dataset, where sediments are very

muddy, compared to the studies of Coull (1999). In fine silt sediment, meiofauna was as abundant as fine sandy medium silt or very coarse sandy fine silt. However, this hypothesis is corroborated with the different size classes of nematodes; small nematode abundance (mainly dominated by 2A feeding type) is positively correlated with higher percentage of mud (fine silt sediment) and OM content, and, inversely, large nematode abundance (mainly dominated by 2B feeding type) is negatively correlated with higher percentage of mud and OM content. Consequently, granulometry and OM content appear to be driving factors of the size structure and functional characteristics of nematodes. Nonetheless, sediment texture is also likely to have a strong structuring influence on nematodes. Thus, in percentage, small nematodes, mainly dominated by epigrowth-feeders nematodes, are more abundant in very fluid mud (Awala St A: 44%) compared to compacted bare mud in front of mangroves (Awala St C: 17%). This result could be explained by the sediment texture in Awala St A—the high fluidity of mud may result in high physical instability of the sediment (tidal currents, wave action, or input of resuspended sediment), causing a large perturbation to the settlement of the meiofauna. The lowest values of Chl a biomass, prokaryotes, and meiofauna abundances were recorded at Awala St A. Thus, the likely high mobility of sediment selects for smaller meiobenthic organisms and epigrowth-feeders nematodes and disturbs the larger organisms in the sediment as omnivorous-carnivorous nematodes (2B). Kapusta et al. (2005) recorded the lowest abundance of meiofauna in unstable sediment in a channel in the Tramandai-Armazem estuary in southern Brazil, and highest abundance of meiofauna, especially large species, in a sheltered area (i.e., seagrass beds). Yamanaka et al. (2013) demonstrated that the most significant factor affecting meiofauna was exposure to waves and currents.

The second postulated hypothesis was that meiofauna was more abundant when biofilm of Chl a and prokaryotes, both representing potential prey for meiofauna, were more abundant. This hypothesis was not corroborated with the present dataset. In this study, no

correlation was found between meiofauna abundance and their potential prey. The interpretation is 1) the bacterivory in meiofauna is considered a minor factor in the regulation of the prokaryote pool, and bacteria do not constitute a preferentially ingested resource (no top-down control of bacteria [Pascal et al., 2008b]); and 2) despite the fact that herbivory is largely extended in meiofauna and confirmed here by the dominance of the epigrowth-feeders (2A) in different stations, the primary production largely supplies their food needs in intertidal mudflats. Finally, meiofauna uses only a negligible part of carbon from primary production (Middelburg et al., 2000; Moens et al., 2002; Pinckney et al., 2003; Rzeznik-Orignac and Fichet, 2012; van Oevelen et al., 2006). Food availability also does not appear to limit meiofaunal abundance (no top-down control of MPB [Coull, 1999]). Furthermore, Tolhurst et al. (2010) did not find a correlation between meiofauna and Chl a biomass. It appears that further investigations are needed to assess the primary production and meiofauna grazing rates in order to obtain reliable data of carbon flux in benthic ecosystems of the coasts of the Guianas.

Soft mudflats are characterised as containing important biofilms of MPB (Du et al., 2009; Herlory et al., 2004; Perkins et al., 2003; Underwood and Kromkamp, 1999; Underwood and Paterson, 2003) and having high meiofaunal abundances (Heip et al., 1985) compared to sandy sediment. In the present study, in banks with muddy sediment of French Guiana and Suriname, the same tendency was found. For example, in stations with fine silt (muddy), Chl a biomass was 9–19 $\mu\text{g Chl a g}^{-1}$ DW sediment but lower in stations exhibiting sandy mud (around 7 $\mu\text{g Chl a g}^{-1}$ DW sediment). Similar values are found in European upper-shore mudflats (8.5–21 $\mu\text{g Chl a g}^{-1}$ DW sediment [Herlory et al., 2004; Orvain et al., 2014; Underwood, 2010]), and lower values are found in sandflats of the Severn estuary (mean of 5 $\mu\text{g Chl a g}^{-1}$ DW sediment [Underwood, 2010]). However, the Chl a data from the literature presented above were obtained from the first 200, 500, or 1000 μm of the surface

sediment, whereas data obtained in this study correspond to the first 2 cm of mud. In this case, the Chl a biomass is likely to have been diluted with sediment devoid of that used for MPB analysis. A supplementary study analysing the top 0.5 mm of the sediment surface in a few stations in French Guiana and Suriname showed that Chl a biomass could reach up to 180 $\mu\text{g Chl a g}^{-1}$ DW sediment in fine silt sediment (Awala St B and St C) and 80 $\mu\text{g Chl a g}^{-1}$ DW sediment in sandy mud sediment (Kourou) (unpublished results, Dupuy, personal communication). This supplementary study demonstrated that in intertidal sandy mud sediments and fine silt sediments of French Guiana and Suriname, primary producer biomass tends to be greater than in other tropical or European flats.

Prokaryotic abundance was within the same range as that of European mudflats (2×10^9 cells cm^{-3} at Brouage (Lavergne et al., 2014; Orvain et al., 2014), and in the review of Schmidt et al. (1998), bacterial abundance remains stable, around 10^9 cells cm^{-3}).

In our study, the meiofaunal community was constituted of only six taxa including small organisms of macrofauna (bivalves and gastropods). In other studies on intertidal flats, number of taxa was variable but in tropical areas tend to welcome more taxa: in Mangrove forest of Vietnam, 11 taxa were described (Xuan et al., 2007) while 7 taxa were recorded in Southeast coast of India (Chinnadurai et al., 2007). In sandy sediment of Maldives in Indian Ocean, from 17 to 20 different taxa were collected (Semprucci et al., 2010; 2011). In temperate area, the number of taxa varied from 4 to 13 taxa (Bohorquez et al., 1997 and Soetaert et al., 1995 respectively) and was similar to our results (7 taxa: Alongi et al., 1987; 6 taxa: Orignac et al., 2003). The hypothesis for explaining the lower number of taxa in tropical mudflat in French Guiana, is that mudflat is highly physically unstable. Few taxa can survive in such fluid mud in the mudbanks.

On Guiana's coast, total abundances of meiofauna were particularly high, ranging from 88–220 ind cm^{-3} (corresponding to 1760 ind 10 cm^{-2} to 4400 ind 10 cm^{-2}) compared with other

studies on intertidal flats, where abundances were lower (1000 ind 10 cm⁻²; Coull, 1999; Heip et al., 1985; Platt and Warwick, 1980). In the Brouage mudflats (Atlantic French coast), the mean abundances were 2000 ind 10 cm⁻² (Rzeznik-Orignac et al., 2003). Similar abundances previously were observed by Montagna et al. (1995) in Marennes Oléron Bay (Atlantic French coast) and by others in European estuaries, such as Gironde, Tagus, and Westerschelde (Soetaert et al., 1995), or the mudflats of the Lynher estuary in Cornwall (Warwick and Price, 1979). Abundances of meiofauna in mangroves provided in the literature correspond to the lower values found in our study: 1156–2082 ind 10 cm⁻² in Vietnam (Xuan et al., 2007); a maximum of 735 ind 10 cm⁻² in mangroves of Nha Trang Bay (Vietnam); (Mokievsky et al., 2011) and 500 ind 10 cm⁻² in a tropical tidal flat of northeastern Australia (Dittman, 2000). The highest value of meiofauna abundance was found by Vanhove et al. (1992), with 6707 ind 10 cm⁻² in the *Bruguiera* mangroves in Gazi Bay (Kenya). In conclusion, meiofauna abundance observed in French Guiana and Suriname was almost always higher than in other world areas, with the exception of mangroves in Gazi Bay (Kenya) (Vanhove et al., 1992).

As a constituent of meiofauna, nematodes represent the most common and abundant taxon in this study. They are also commonly found in European Atlantic mudflats (Montagna et al., 1995; Platt and Warwick, 1980; Rzeznik-Orignac et al., 2003) and mangrove ecosystems (Alongi, 1989; Chinnadurai and Fernando, 2007; Mokievsky et al., 2011; Xuan et al., 2007). Nematodes seem to be less prominent in Cuban mangroves (Lalana-Rueda and Gosselck, 1986) and Cape York Peninsula mangroves in Australia (Alongi, 1987).

Harpacticoid copepods are usually found as the second-most common taxon in terms of occurrence but are present at much lower abundances compared to nematodes in this study. Copepods are more related to coarse or sandy sediments in tropical area (Semprucci et al., 2010), or mangrove ecosystems (Chinnadurai and Fernando, 2007; Xuan et al., 2007) or in

many European mudflats (Montagna et al., 1995; Platt and Warwick, 1980; Rzeznik-Orignac et al., 2003).

Interestingly, and, for the first time on bare mudflat habitat, no foraminifera were found among the six studied stations. Indeed, foraminifera mainly were found in the mangroves with a richness reaching up to 44 species and abundances reaching up to 2000 foraminifera 50 cm^{-3} , but they were rare or absent in the open mudbanks (Debenay et al., 2002). The hypothesis for explaining the unexpected absence of this taxa is that the high physical instability of the mudflat does not allow foraminifera to survive in such fluid mud in the mudbanks as previously related by Debenay et al. (2002). Nevertheless, this hypothesis must be tested by experimental approach.

Further studies in this area are needed in order to better describe the local species richness of the meiofauna, and especially for nematodes. This presents a difficult challenge, since very few data from coasts of the Guianas are available, and many species will have to be described.

5. Conclusions

On coasts of the Guianas, in the North Atlantic coast of South America in sandy mud sediment and fine silt sediment, biomass of primary producers tended to be greater toward the other world areas, and meiofauna abundance data were almost always higher, despite the high instability of mudflats. Meiofauna was not more abundant when the sediment was composed of the finest sediment particles and also when Chl *a* and prokaryotes, potential preys of meiofauna, were greater. But, epigrowth-feeders (2A) nematodes and small ones (biomass of $0.07 \pm 0.001 \mu\text{g ind}^{-1}$) were largely well adapted in very fluid and unstable mud stations with probably no limitation of food source (e.g. microphytobenthos). No foraminifera were found among the six stations of the study. Very fluid mud with physical instability of sediment

caused a large perturbation for the settlement of meiofauna; the least amounts of Chl a biomass and prokaryotic and meiofauna abundances were found there. Thus, the probable mobility of sediment may select for smaller meiobenthic organisms and disturb the larger organisms in the sediment, and, therefore, would not permit the settlement of foraminifera. In addition, temporary meiofauna (e.g. very small macrofauna) largely was found in the sediment.

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Fig. 1: Map showing the study area and location of samples collected in French Guiana and Suriname.

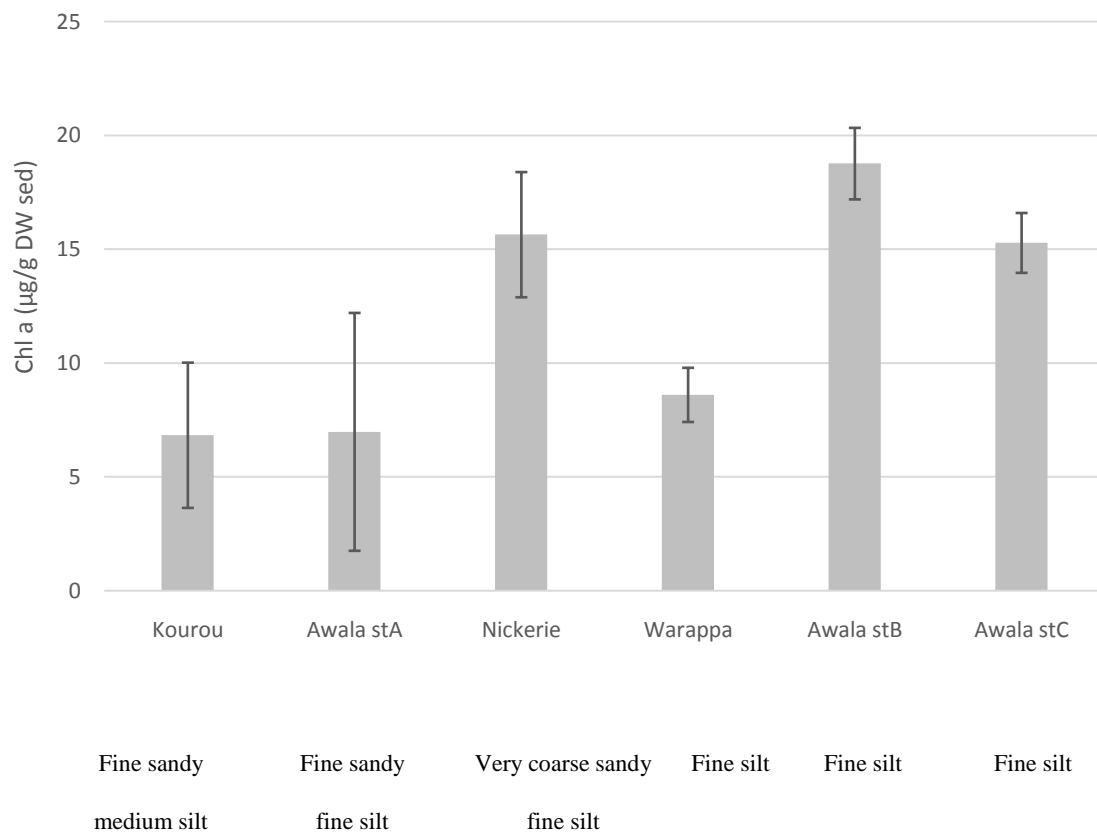


Fig. 2: Chlorophyll *a* (Chl *a*) biomass (mean \pm SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st= station.

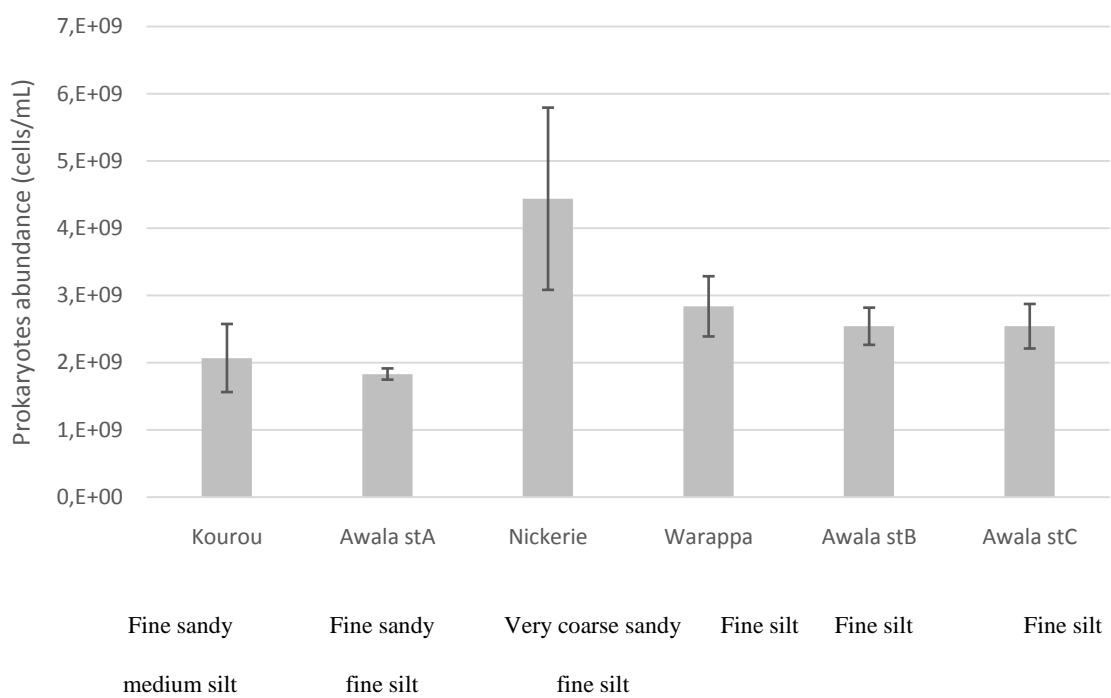


Fig. 3: Prokaryote abundance (mean \pm SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st= station.

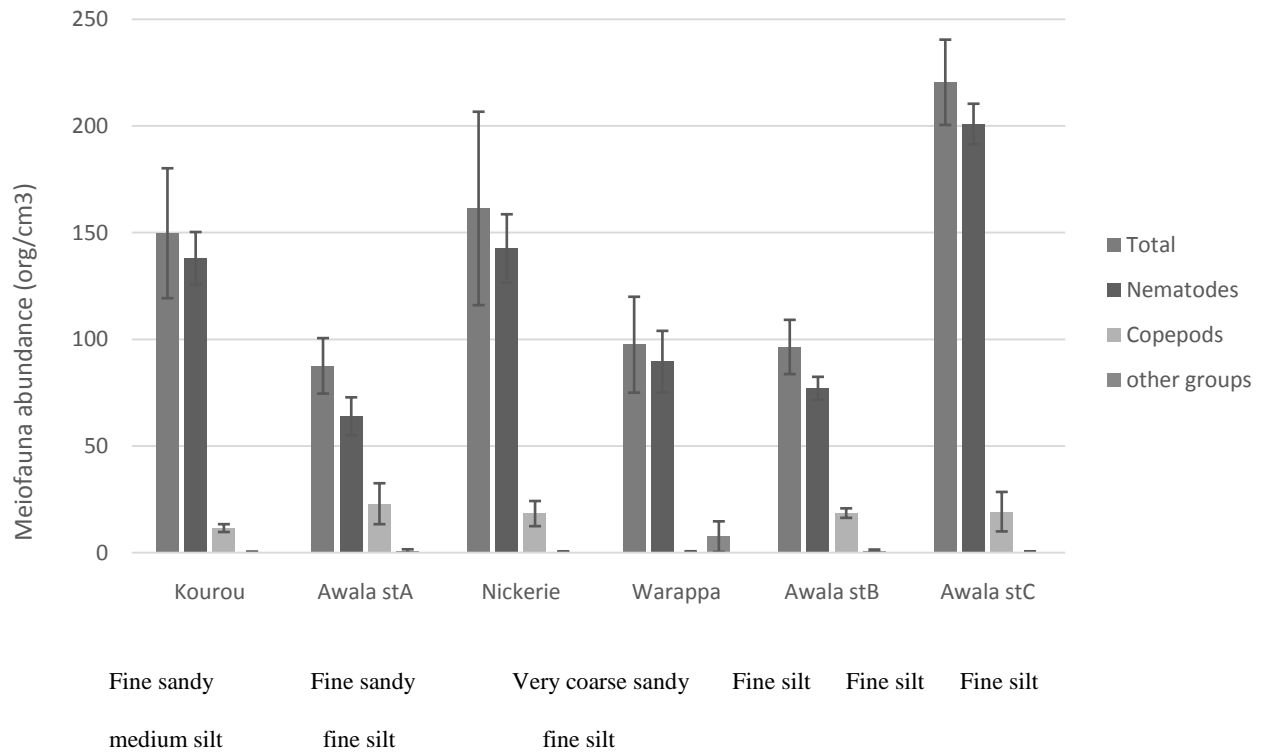


Fig. 4: Meiofauna abundance (mean \pm SD) of the top 2 cm of sediment at different stations in French Guiana and Suriname areas, classified according to sediment type. st= station. Other groups= sum of plathelminthes, ostracodes, small gastropods and small bivalves.

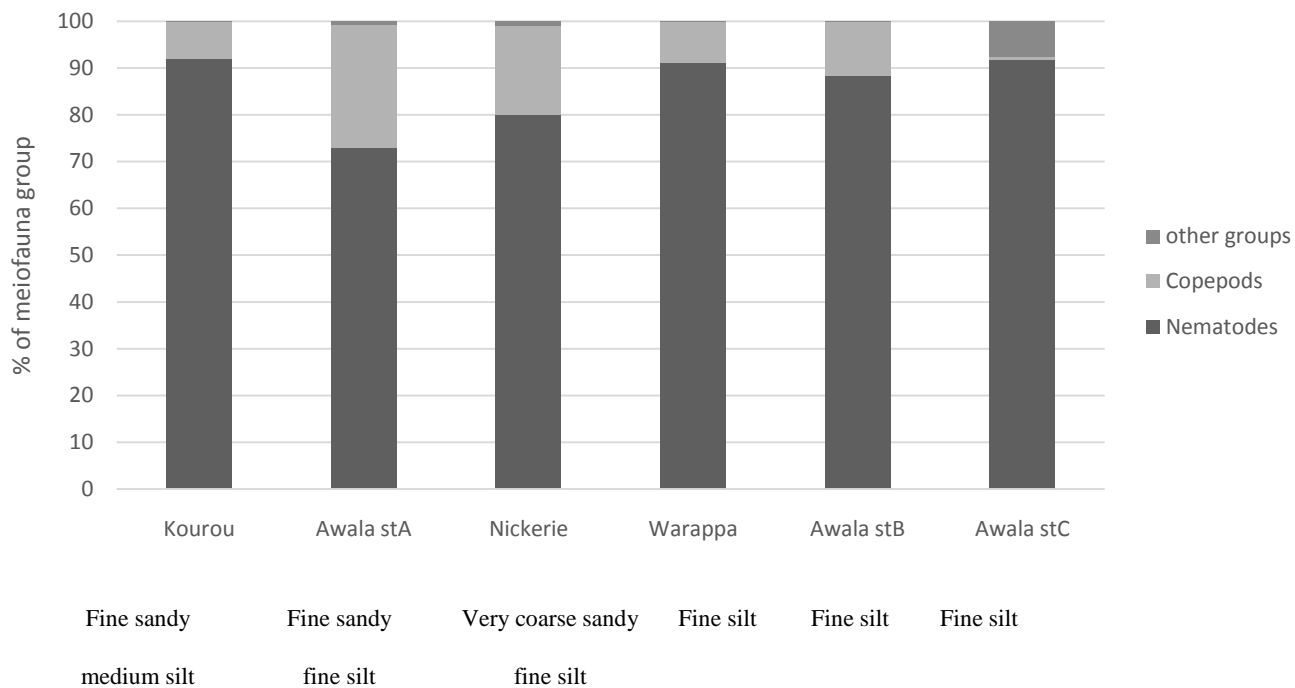


Fig. 5: Percentage of meiofauna group at different stations in French Guiana and Suriname areas, classified according to sediment type. st= station. %= percentage. Other groups= sum of plathelminthes, ostracodes, small gastropods and small bivalves.

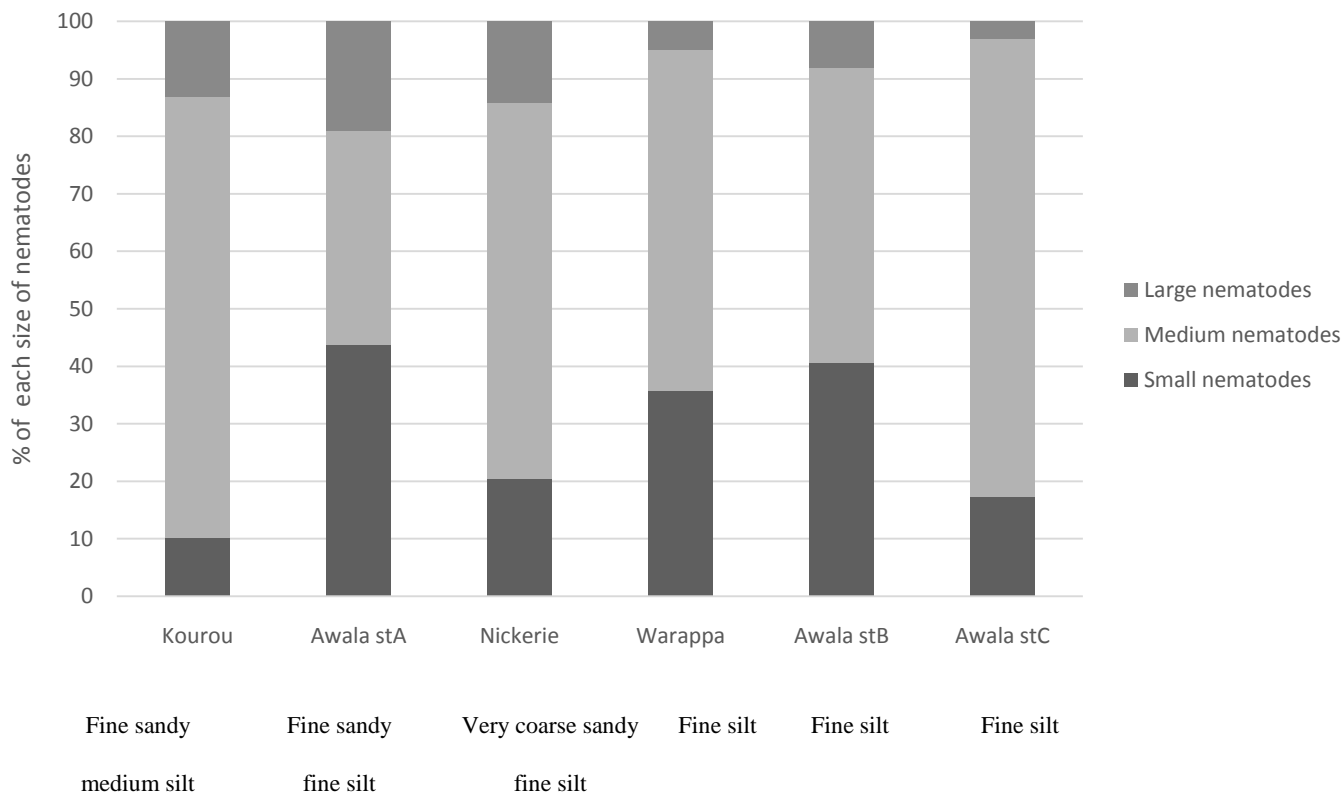


Fig. 6: Percentage of the size classes of nematodes at different stations in French Guiana and Suriname areas, classified according to sediment type. Classifications were as follows: small nematodes (mean length: $300 \pm 30 \mu\text{m}$; mean width: $18 \pm 5 \mu\text{m}$); medium nematodes (mean length: $695 \pm 130 \mu\text{m}$; mean width: $26 \pm 9 \mu\text{m}$); and large nematodes (mean length: $1500 \pm 160 \mu\text{m}$; mean width: $75 \pm 10 \mu\text{m}$). st= station. %= percentage.

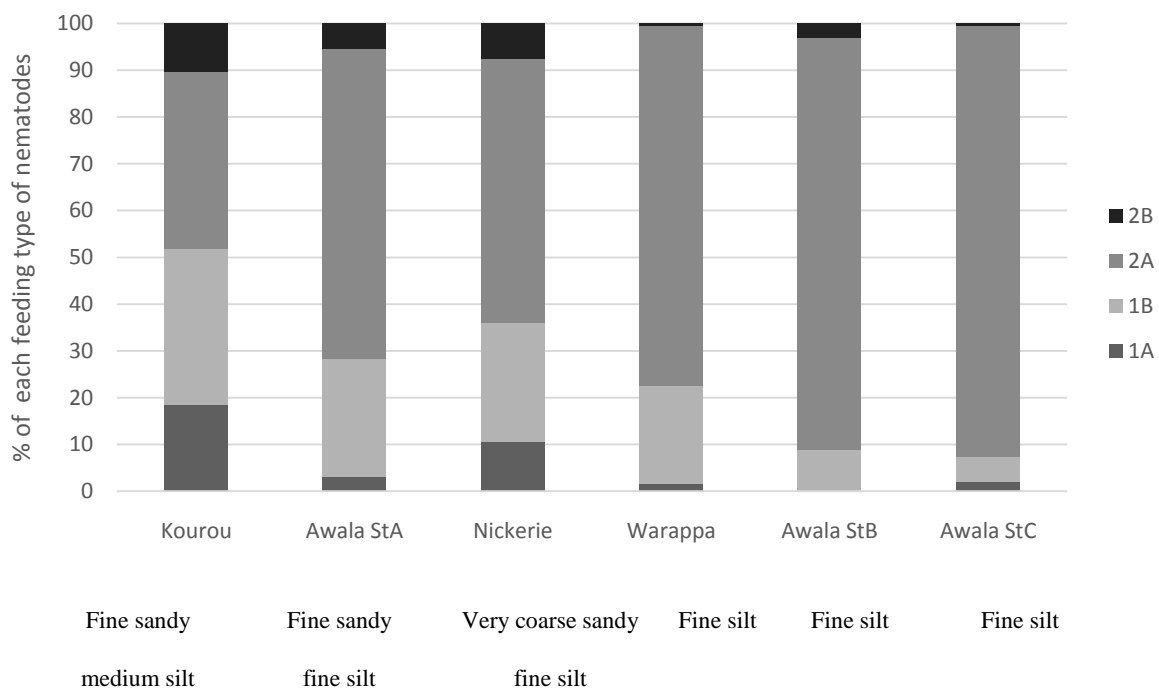
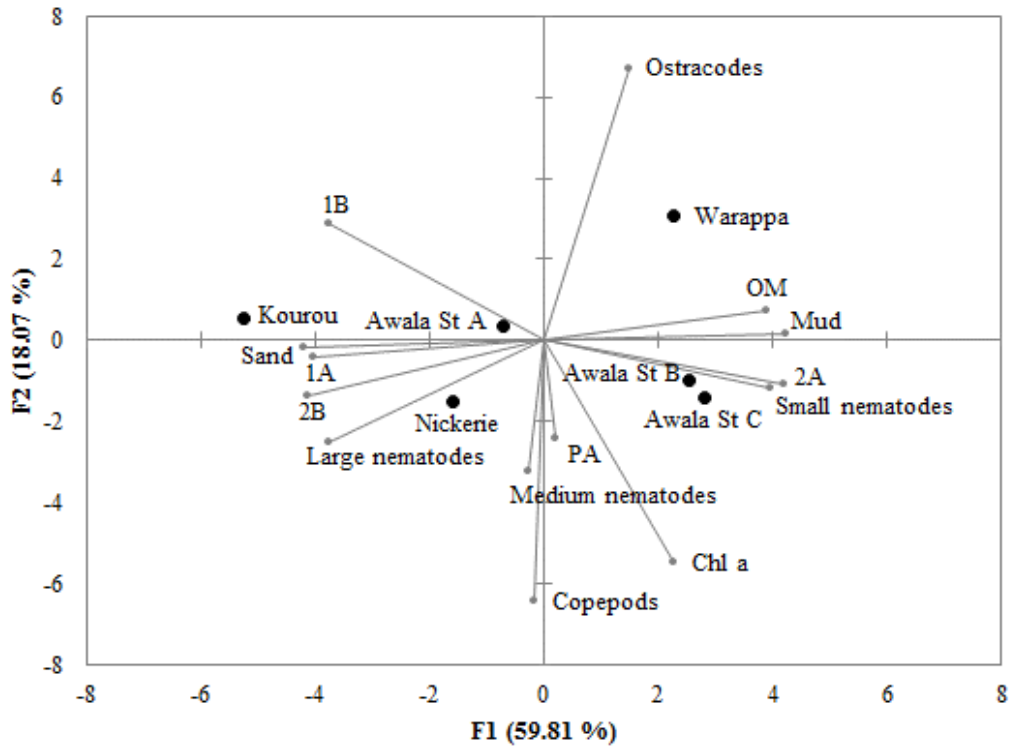


Fig. 7: Percentage of each feeding type of nematodes at different stations in French Guiana and Suriname areas, classified according to sediment type. 1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epigrowth feeders; 2B, omnivorous-carnivorous. st= station. %= percentage.

A

Biplot (axes F1 and F2 : 77.88 %)



B

Biplot (axes F1 and F3 : 70.81 %)

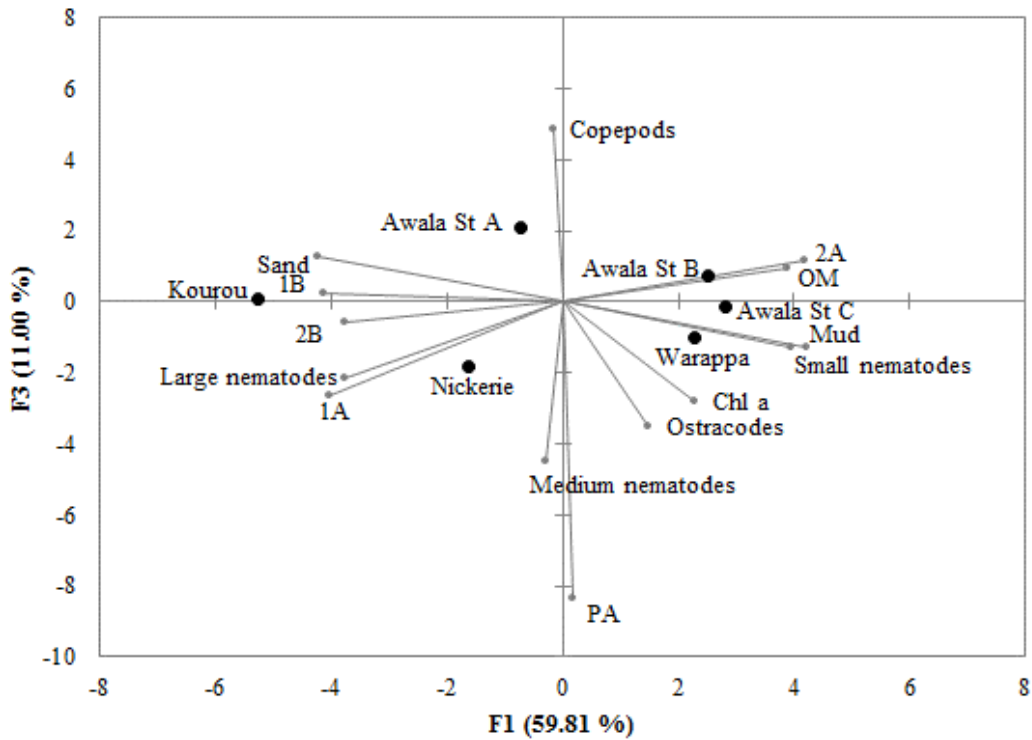


Fig. 8: Principle component analyses calculated using six observations (samples of six sites: Kourou, Nickerie, Warappa, and Awala Stations A, B, and C) and 14 variables (mud, sand, OM, PA, Chl a, small, medium, and large nematods, copepods, and ostracodes abundance, and the 4 feeding type of nematodes). A) Biplot F1 × F2 and B) biplot F1 × F3. For each variable, the circle of correlation is reported. Observations were reported in the circle of correlation. Abbreviations: Chl a: chlorophyll *a* biomass; mud: percentage of mud; sand: percentage of sand; OM: organic matter mass; PA: prokaryotic cell numbers; 1A, 1B, 2A and 2B: feeding guilds of nematodes (see material and methods part for details); st= station.

Table 1: Granulometric parameters and organic matter content (OM) (%) of the different stations in French Guiana and Suriname areas.

Station	Mud (%)	Sand (%)	Mean grain size (µm)	Median grain size (µm): D 50	Sample type	Textural group	Sediment name	OM (%)
Kourou	81	19	14.08	10.96	Bimodal	Sandy mud	Fine sandy medium silt	4.44
Awala St1	88.76	11.24	7.96	5.86	Bimodal	Sandy mud	Fine sandy fine silt	5.99
Nickerie	89.65	10.35	9.75	6.54	Bimodal	Sandy mud	Very coarse sandy fine silt	5.55
Warappa	99.78	0.22	5.45	5.15	Unimodal	Mud	Fine silt	6.21
Awala St4	99.92	0.08	5.62	5.51	Unimodal	Mud	Fine silt	6
Awala St5	100	0	5.48	5.45	Unimodal	Mud	Fine silt	5.99

Table 2: Pearson's correlations and p-values between environmental variables and meiofauna. PA= Prokaryotes abundance; Chl a= Chlorophyll a biomass; 1A, 1B, 2A and 2B; feeding guilds of nematodes (see material and methods part for details).

Pearson's correlation

Variables	PA	Chl a	OM	Small nematodes	Medium nematodes	Large nematodes	Copepods	Ostracodes	Mud	Sand	1A	1B	2A	2B
PA	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Chl a		1	-	-	-	-	-	-	-	-	-	-	-	-
OM			1	0.935	-	-	-	-	0.847	-0.847	-0.96	-	0.851	-
Small nematodes				1	-	-	-	-	0.894	-0.894	-0.884	-	0.893	-
Medium nematodes					1	-	-	-	-	-	-	-	-	-
Large nematodes						1	-	-	-0.871	0.871	0.848	-	-0.865	0.921
Copepods							1	-0.882	-	-	-	-	-	-
Ostracodes								1	-	-	-	-	-	-
Mud									1	-1	-0.883	-	0.952	-
Sand										1	0.883	0.877	-0.952	0.954
1A											1	-	-0.927	0.894
1B												1	-0.95	-
2A													1	-
														0.928

P-Values

Variables	PA	Chl a	OM	Small nematodes	Medium nematodes	Large nematodes	Copepods	Ostracodes	Mud	Sand	1A	1B	2A	2B
PA	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Chl a		0	-	-	-	-	-	-	-	-	-	-	-	-
OM			0	0.006	-	-	-	-	0.033	0.033	0.002	-	0.031	0.023
Small nematodes				0	-	-	-	-	0.016	0.016	0.019	-	0.016	0.022
Medium nematodes					0	-	-	-	-	-	-	-	-	-
Large nematodes						0	-	-	0.024	0.024	0.033	-	0.026	0.009
Copepods							0	0.019	-	-	-	-	-	-
Ostracodes								0	-	-	-	-	-	-
Mud									0	<0.0001	0.019	0.021	0.003	0.003
Sand										0	0.019	0.021	0.003	0.003
1A											0	-	0.007	0.016
1B												0	0.003	-
2A													0	0.007

